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# Variations in soil nutrient availability across Tibetan grassland from the 1980s to 2010s

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ABSTRACT

Changes in soil nutrient availability attributed to climate change and associated permafrost degradation have been reported in several ecosystems. However, little is known about the changes of soil nutrient availability in alpine grassland ecosystems. Based on a comprehensive dataset and random forest models, we investigated soil available nutrients changes and their relationships with environmental factors for the top 10 cm soils across Tibetan grassland between the 1980s and 2010s. During this period, topsoil available nitrogen stocks increased significantly by 24%, while available phosphorus and potassium stocks decreased significantly by 3% and 23%, respectively. Topsoil nutrient availability dynamics varied substantially among vegetation types. Initial nutrient stocks explained the largest proportions of available nutrients changes, though climate, permafrost, vegetation, soil properties, and their interactions also had significant contributions. The increasing rate of active layer thickness was negatively related to soil available nitrogen dynamics but did not significantly change available phosphorus and potassium, indicating that the increase in the annual depth of surface thaw of the permafrost was associated with an increase in soil nitrogen availability but no significant changes in available phosphorus and potassium. These results suggest that the Tibetan alpine grassland ecosystems may shift from nitrogen-limited to phosphorus or potassium-limited in the future.

## 1. Introduction

Soil nutrient availability plays essential roles both in linking soil to plant and in regulating nutrient cycling in terrestrial ecosystems (Sistla and Schimel, 2012). Nitrogen (N), phosphorus (P), and potassium (K) are the prevailingly competitive nutrient-resources among plant communities (Craine and Dybzinski, 2013), limiting plant growth and production (Matías et al., 2011). Changes in nutrient availability could affect ecosystem structure and functions through altering plant diversity and species (Fernández-Martínezl et al., 2014). In permafrost regions, it has also been reported that the elevated plant-available N caused by permafrost degradation could increase aboveground biomass (Schuur et al., 2007; Natali et al., 2012; Salmon et al., 2016). Therefore, it is important to investigate the spatio-temporal variations of soil nutrient availability in cold ecosystems under various climate change scenarios.

Available nutrients in soils under natural conditions are controlled by several factors, such as climate, parent materials, weathering, microbial activity, habitat structure, and atmospheric deposition (Whitehead, 2000; Matías et al., 2011). Changes in temperature and rainfall have been observed to instigate an imbalance of soil nutrients or decoupling of soil nutrients cycling through altering soil moisture, ground temperature, and microbial activities (Peñuelas et al., 2013; Mooshammer et al., 2017; Yue et al., 2017). Many arid regions of the

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world are expanding as the climate warms, with drastic repercussions on biological and abiotic processes (Wardle, 2013), revealing that increased aridity is often associated with a decrease in available N and an increase in available P (Delgado-Baquerizo et al., 2013). During the past decades, elevated N deposition has been documented to significantly enhance plant N status across China (Liu et al., 2013). These findings suggest that as nutrients become less available, an associated decline in carbon stores and nutrient cycling are expected in natural environments (Peñuelas et al., 2013), thus may shift nutrient limitation and ecological functions. Nevertheless, the extent that climate change and atmospheric deposition alter soil nutrients and plant-soil feedback remains unclear, particularly in cold ecosystems.

Permafrost degradation including increased permafrost temperature and deepened active layer thickness has been observed across the cold regions of the world during the last several decades (IPCC, 2013). This process may release soil nutrients that are available to plant growth because warming increases nutrient mineralization and microbial decomposition (Salmon et al., 2016; Keuper et al., 2017). A significant increase in available N has been documented and attributed to thawing permafrost in high-latitude ecosystems, including peatlands of subarctic Sweden (Keuper et al., 2012, 2017), boreal and tundra ecosystems of interior Alaska (Natali et al., 2012; Finger et al., 2016; Salmon et al., 2016). Moreover, Harms and Jones (2012) reported an increase in inorganic N exported from thawing permafrost soils into streams in an arctic catchment, and Schuur et al. (2007) documented enhanced N availability by plant uptake due to permafrost degradation. However, these studies focused on permafrost and nutrient dynamics from in-situ and short-term manipulative experiments with limited application over the long term, which hinders our ability to gain further insight into future long-term ecosystem change.

The Tibetan Plateau has experienced permafrost degradation in recent decades (Zhao et al., 2010). Permafrost in this region has a thicker active layer (> 2 m; Pang et al., 2009) compared to that in circumpolar regions (~0.5 m; Mishra and Riley, 2014). Associated with warming climate and degraded permafrost are a decrease in topsoil moisture through enhancing leaching and evapotranspiration (Xue et al., 2017; Mu et al., 2018), which may alter topsoil nutrients dynamics. Nonetheless, there is limited information regarding the effect of climate warming and thawing permafrost on soil nutrient availability in the Tibetan ecosystem. This study was to evaluate and quantify temporal changes in soil nutrient availability under different vegetation types across Tibetan grassland, using in-situ measurements completed during the 1980s (319 sites) and sampled again during the 2010s (253 sites). We used machine-learning algorithms to obtain measurements of available nutrients for comparison between the study periods. Moreover, these data were also used to estimate trends in available nutrients as influenced by climate, vegetation, permafrost, and other edaphic factors.

## 2. Materials and methods

### 2.1. Study area

Permafrost underlies an area of $1.06 \times 10^6$ km$^2$ in the Tibetan Plateau (Fig. 1; Zou et al., 2017). Where present, permafrost is characterized by thick active layers (from 1.32 to 4.57 m; Pang et al., 2009). Mean annual temperature (MAT) varies from −9.7 to 6.8 °C across this region and has been increasing at a rate of 0.02–0.04 °C/yr during the last five decades (Yang et al., 2017), and mean annual precipitation (MAP) ranges between 84 and 700 mm. The vegetation types in alpine ecosystem are dominated by swamp meadow, meadow, steppe, and desert (Wang et al., 2017), and soil orders based on *US Soil Taxonomy* mainly consist of Gelisols, Inceptisols, Mollisols, Aridisols, and Entisols (Li et al., 2015).

### 2.2. Soil data collection and analyses

Three separated soil profile datasets were used to investigate the temporal variations in topsoil (0–10 cm layer) available nutrients stocks across the Tibetan grassland (Fig. 1). The first is a part of the Second National Soil Inventory in China completed during the 1980s and the second and third from soil samples collected during the 2010s. A total of 572 sampling sites were incorporated in the composite database including 228 sites were from permafrost regions (50 sites from swamp meadow, 62 from meadow, 61 from steppe, and 55 from desert) and 344 sites were from seasonally frozen ground (114 sites from meadow, 171 from steppe, and 59 from desert).

The first dataset included 319 soil profiles (Fig. 1) obtained from the National Earth System Science Data Sharing Infrastructure, National Science & Technology Infrastructure of China (http://www.geodata.cn), which records the key available nutrients and relevant physical properties in soils (Shangguan et al., 2013; Pan and Shi, 2015). The second dataset included 208 sites representing major vegetation types across the Tibetan Plateau (Fig. 1), conducted by Cryosphere Research Station on the Qinghai-Tibetan Plateau from 2009 to 2011. Soil samples at each site were collected at specific depth intervals (e.g. 0–10, 10–20, 20–30 cm, etc.). Due to the possible heterogeneity in soil physical properties, several samples were mixed as one composite sample (at least 1 kg soils) and then divided into three subsamples for measuring soil available nutrients. In addition, for the 2010s period, we also employed a soil database (Fig. 1) that includes 45 sites distributed in the eastern Tibetan Plateau and published by Geng et al. (2017).

For all three datasets, key chemical and physical soil properties including available N, P, and K, layer thickness, pH, and soil texture were analyzed. Standardization of the various datasets was accomplished by using a depth-weighted method to convert available nutrients of horizon-based to depth-based values. Bulk density was determined by an empirical equation ($BD = 0.49 + 1.09\exp(-0.0235SOC)$, $R^2 = 0.74$, $P < 0.001$; Fig. S1) when the specific layers were not measured, and this method has been proved to be reliable (Xu et al., 2016). For sites lacking gravel content data, we extracted the gravel content value for each sampling site using the 30 × 30 arc-second resolution gridded product that was mapped based on 8979 soil profiles from China's Second National Soil Inventory (Shangguan et al., 2013).

Soil bulk density was estimated with the metal-ring method. Soil particle size distribution was analyzed with a SEDIMAT4-12 Analyzer. Soil pH was determined using a glass electrode with a soil-to-water ratio of 1:5. Analogous to the historical survey, available phosphorus (AP) and available potassium (AK) were measured with the $NaHCO_3$ extraction/Mo-Sb colorimetric method and $NH_4OAc$ extraction/flame photometer method, respectively (Lu, 2000). For the 1980s dataset, soil available N (AN) was measured by Conway diffusion method (National Soil Survey Office, 1992); however, due to the limited measurements of (AN) for most sampling sites during the 2010s, we utilized an empirical eq. ($AN = 67.83TN + 10.16$, $R^2 = 0.78$, $P < 0.0001$; Fig. S2) to estimate AN when it was not measured.

### 2.3. Climate, vegetation, and permafrost information

MAT and MAP products at a resolution of 0.5° × 0.5° were obtained from the National Meteorological Information Center (2012a, 2012b) during 1961–2014. Data point coordinates were intersected with the MAT and MAP products to determine MAT and MAP values for each site location. We estimated the normalized difference vegetation index (NDVI) at a site scale by calculating the mean NDVI data for the growing season. The original NDVI dataset was obtained from the multiple Advanced Very High-Resolution Radiometer daily observations (Tucker et al., 2005). In addition, to identify the relationship between permafrost degradation and soil available nutrient changes, the long-term data of active layer thickness along the Qinghai-Tibetan

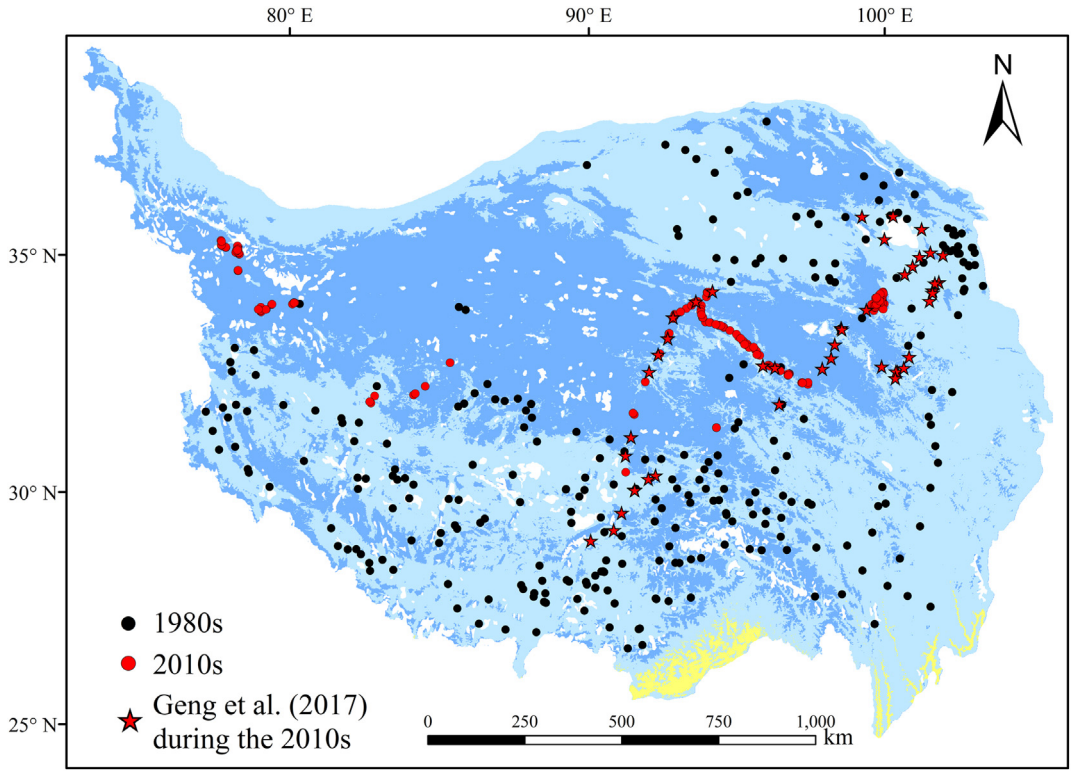


**Fig. 1.** Distribution of sampling sites, permafrost, and seasonally frozen ground across the Tibetan grassland. The red circles represent sites sampled during the 2010s. The red stars indicate sites sampled during the 2010s obtained by Geng et al. (2017). The black circles represent sites sampled during the 1980s as part of the Second National Soil Inventory in China (Pan and Shi, 2015). Areas of permafrost are represented in dark blue, with areas of seasonally frozen ground by light blue and frost free areas indicated in yellow (Zou et al., 2017). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Highway were acquired from the Cryosphere Research Station on the Qinghai-Tibetan Plateau, Chinese Academy of Sciences. Moreover, wet N deposition values are derived from precipitation, and it can be estimated from the following statistical equation synthesized by a comprehensive dataset available for China (Liu et al., 2013; Yang et al., 2015):

$N_{dep} = 3.6281\exp^{0.001MAP}$, $R^2 = 0.22$, $P < 0.05$where $N_{dep}$ represents wet N deposition rate and MAP is an abbreviation for mean annual precipitation.

### 2.4. Statistical analyses

A pairing of sites from the two sampling periods was necessary to compare temporal changes in soil available nutrients from the 1980s to 2010s. Where temporal pairing was not possible, we used random forest (RF) models to generate nutrient values for the missing sites from each period. The basic modeling process included using available nutrients data in conjunction with relevant environmental factors (e.g. latitude, longitude, altitude, MAT, MAP, NDVI, pH, and soil texture) to generate missing nutrient data values. As a part of the modeling processes, the observed data were divided into two groups: 90% of the data were used as a training dataset to construct the RF models and the remaining data to assess the performance of those models. Random forest models were performed with "randomForest" packages (Liaw and Wiener, 2002) in R software (R Development Core Team, 2014). The high correlation between the observed and predicted available nutrients confirmed a reliable prediction of the machine-learning algorithms during both periods (Fig. S3). This approach was also successfully applied to detect the soil organic carbon and N:P ratios dynamics (Yang et al., 2014; Chen et al., 2016).

To improve the distribution of homogeneity of variance, soil available nutrients were $\log_{10}$-transformed and their changes were converted using z-score method during the statistical analyses. Two-way analysis of variance (ANOVA) and Tukey's post hoc tests were used to identify the variations in soil available nutrients among vegetation types and frost status between the 1980s and 2010s. Nutrient data from different periods with total grassland were analyzed using one-way ANOVA. Ordinary least squares were used to estimate the relationships between soil nutrient availability dynamics and environmental factors. General linear models were applied to estimate integrative impacts of environmental factors on soil available nutrients changes.

## 3. Results

### 3.1. Temporal dynamics of soil nutrient availability

Temporal changing magnitudes of topsoil available nutrients differed among vegetation types and frost status. On average, soil AN stock significantly increased from 11.94 to 14.80 g/m$^2$ across the Tibetan grassland during the last three decades, while both AP and AK stocks significantly decreased from 0.67 to 0.65 g/m$^2$ and from 17.26 to 13.24 g/m$^2$, respectively (Fig. 2). More specifically, AN stocks increased significantly in swamp meadow (12.93 g/m$^2$), meadow (3.63 g/m$^2$), and steppe (1.58 g/m$^2$), but it did not change in desert; soil AP stock exhibited a significant increase in both swamp meadow (0.61 g/m$^2$) and meadow (0.27 g/m$^2$), while it decreased significantly in steppe ($-0.20$ g/m$^2$) and desert ($-0.38$ g/m$^2$); uniform decreases in AK stock were observed among vegetation types from the 1980s to 2010s (2.83–5.22 g/m$^2$; Fig. 2). Furthermore, the two-way ANONA results showed that vegetation types, years, and their interaction significantly affected soil available nutrients over the Tibetan grassland, with an exception of the effects of years on AP (Table S1).

The changing directions of soil available nutrients over the sampling interval were almost uniform under the presence or absence of

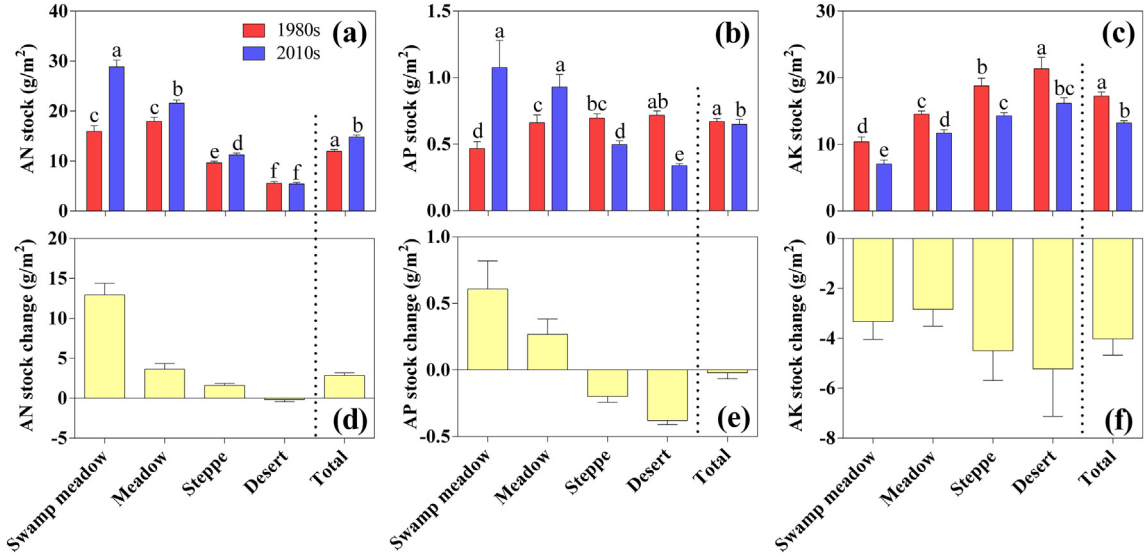


**Fig. 2.** Soil available nutrients stocks (a–c) in the top 10 cm soils under different vegetation types across the Tibetan grassland during the 1980s and 2010s, and their corresponding net changes (d–f). Same letters indicate non-significant differences within each figure (left side of dotted line), and error bars express standard errors of mean values. The right side of dotted line indicate that the differences between sampling periods for the whole Tibetan grassland. AN, available nitrogen; AP, available phosphorus; AK, available potassium.

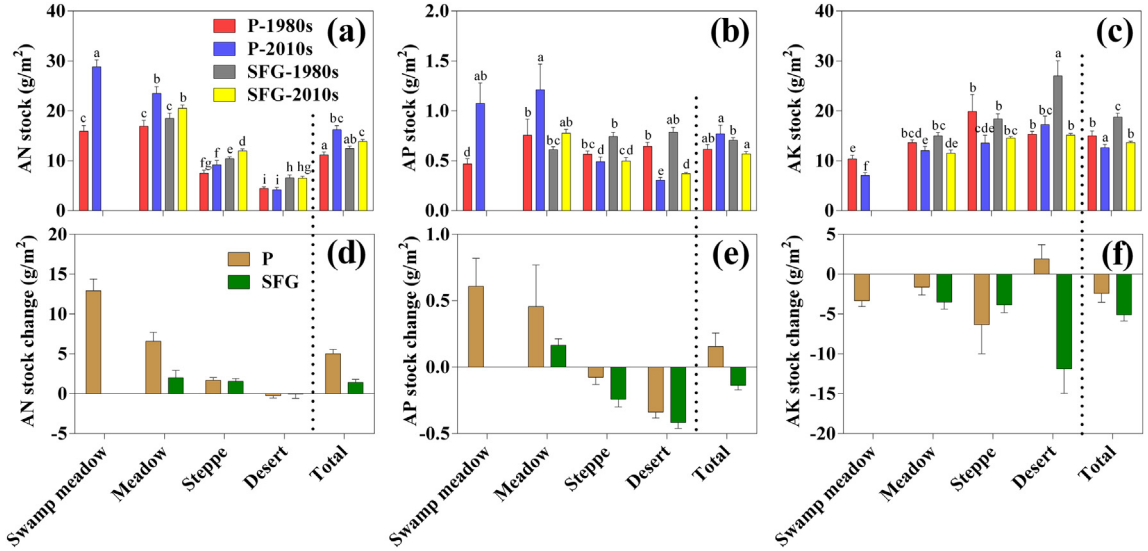


**Fig. 3.** A comparison of soil available nutrients stocks (a–c) in the top 10 cm soils under different vegetation types and frost status across the Tibetan grassland during the 1980s and 2010s sampling periods. Same letters indicate non-significant differences within each figure (left side of dotted line), and error bars express standard errors of mean values. The right side of dotted line indicate that the differences between sampling periods and frost status for the whole Tibetan grassland. Net changes in nutrient stocks are illustrated for each vegetation type (d–f). Abbreviations are defined as follows: AN, available nitrogen; AP, available phosphorus; AK, available potassium; P, permafrost; SFG, seasonally frozen ground.

permafrost over the Tibetan grassland (Fig. 3). Across all of the sites, soil AN stock increased significantly by 44.9 and 11.5% for permafrost and seasonally frozen ground regions, respectively (Fig. 3a, d). Soil AP stocks increased insignificantly by 25.3% for permafrost regions, whereas it decreased significantly by 19.4% for the land with seasonally frozen ground (Fig. 3b, e). In contrast, soil AK stock significantly decreased by 16.0 and 27.2% for permafrost and seasonally frozen sites, respectively (Fig. 3c, f). However, the changing magnitudes of soil available nutrients under permafrost and seasonally frozen ground regions also varied among vegetation types. For instance, desert sites from within permafrost regions experienced an insignificant increase in soil AK stock for permafrost regions (12.5%) but showed a significant decrease (−44.0%) for regions without permafrost from the 1980s to 2010s (Fig. 3f). Moreover, the ANOVA showed that main effects of frost status, vegetation types, and year on soil available nutrients were significant (Table S2). Both the interactions of frost status and vegetation types, and vegetation types and year significantly affected AN and AP but without significantly influences on AK. The interaction of frost status, vegetation types, and year showed a contrast pattern (Table S2). However, the interaction of frost status and years showed no significant effects on soil available nutrients (Table S2).

### 3.2. Factors influencing soil nutrient availability dynamics

Soil AN dynamic over the entire Tibetan grassland was weakly and positively related to MAT, MAP, N deposition, NDVI, and clay content ($P < 0.05$; Fig. S4, S5), and weakly and negatively correlated with soil pH and bulk density ($P < 0.05$; Fig. S5). Whereas no correlation was

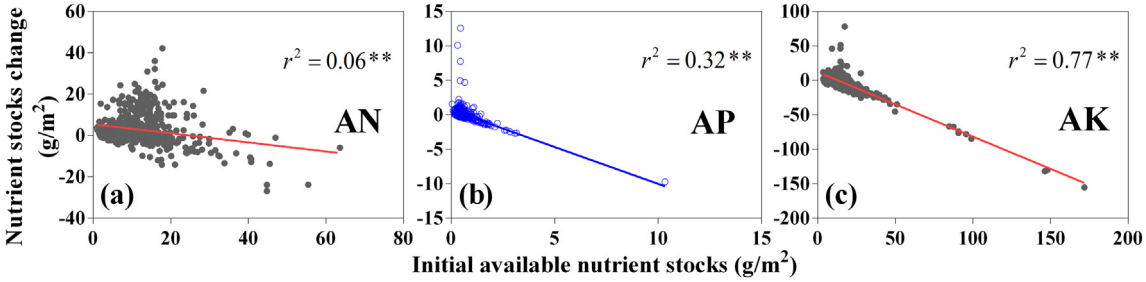


**Fig. 4.** Relationships between available nutrients changes and initial available nutrients for the top 10 cm soils across the Tibetan grassland. AN, available nitrogen; AP, available phosphorus; AK, available potassium; ** indicates significant relationship at $P < 0.01$.

**Table 1**
Effects of environmental factors and initial available nutrients on changes in topsoil available nutrients across the Tibetan grassland using general linear models.

| Environmental factors | AN change | | | AP change | | | AK change | | |
|---|---|---|---|---|---|---|---|---|---|
| | M.S. | F | S.S. (%) | M.S. | F | S.S. (%) | M.S. | F | S.S. (%) |
| PER-type | 0.28 | 0.54 | 0.05 | 1.65 | 2.85 | 0.29 | 0.01 | 0.03 | 0.00 |
| VEG-type | 17.70 | 34.15 | **9.30** | 1.94 | 3.37 | **1.02** | 0.09 | 0.45 | 0.05 |
| MAT | 1.10 | 2.13 | 0.19 | 6.63 | 11.50 | **1.16** | 2.70 | 13.28 | **0.47** |
| MAP | 0.01 | 0.01 | 0.00 | 0.38 | 0.66 | 0.07 | 0.19 | 0.94 | 0.03 |
| $N_{dep}$ | 0.01 | 0.02 | 0.00 | 0.32 | 0.55 | 0.06 | 0.18 | 0.88 | 0.03 |
| NDVI | 0.32 | 0.61 | 0.06 | 0.58 | 1.01 | 0.10 | 0.15 | 0.75 | 0.03 |
| pH | 1.15 | 2.22 | 0.20 | 16.86 | 29.22 | **2.95** | 3.14 | 15.46 | **0.55** |
| Silt | 0.42 | 0.80 | 0.07 | 1.15 | 1.99 | 0.20 | 0.07 | 0.36 | 0.01 |
| Clay | 2.17 | 4.19 | **0.38** | 1.49 | 2.59 | 0.26 | 0.00 | 0.02 | 0.00 |
| Nutri-1980s | 93.70 | 180.74 | **16.41** | 161.54 | 280.10 | **28.30** | 376.25 | 1850.65 | **65.89** |
| PER-type × VEG-type | 4.49 | 8.65 | **1.57** | 1.98 | 3.44 | **0.69** | 0.40 | 1.94 | 0.14 |
| PER-type × VEG-type × MAT × MAP | 0.90 | 1.73 | 1.10 | 0.76 | 1.32 | 0.93 | 0.06 | 0.31 | 0.08 |
| VEG-type × NDVI | 4.10 | 7.90 | **2.15** | 1.38 | 2.39 | 0.72 | 0.02 | 0.09 | 0.01 |
| VEG-type × MAT × MAP × NDVI | 1.35 | 2.61 | **0.95** | 0.44 | 0.77 | 0.31 | 0.09 | 0.46 | 0.07 |
| MAP × Ndep | 0.03 | 0.05 | 0.00 | 0.13 | 0.22 | 0.02 | 0.13 | 0.65 | 0.02 |
| MAP × pH | 0.29 | 0.55 | 0.05 | 4.69 | 8.13 | **0.82** | 0.59 | 2.92 | 0.10 |

Bold fonts indicate $P < 0.05$. AN, available nitrogen; AP, available phosphorus; AK, available potassium; M.S., mean square; S.S., percentage of sum square explained; PER-type, frost status, including permafrost and seasonally frozen ground; VEG-type, vegetation types, including swamp meadow, meadow, steppe, and desert; MAT, mean annual temperature; MAP, mean annual precipitation; $N_{dep}$, nitrogen deposition; NDVI, normalized difference vegetation index; Nutri-1980s, initial available nitrogen, phosphorus, and potassium (1980s) for AN change, AP change, and AK change, respectively.

established between AN changes and silt content (Fig. S5). Soil AP stock dynamic was weakly related to NDVI, soil pH, bulk density, and silt content ($P < 0.05$; Fig. S4, S5), and no significant correlations were observed with MAT, MAP, N deposition, and clay content (Fig. S4, S5). Soil AK change was associated with soil variables (i.e. soil texture; Fig. S5), but it did not change with climatic factors, N deposition, and vegetation index (Fig. S4). Additionally, soil available nutrients changes were negatively correlated with initial available nutrients measurements over the Tibetan grassland (Fig. 4). The general linear models analyses revealed that initial available nutrients (1980s) largely explained the total variations in available nutrients dynamics across alpine ecosystem (16.4% for AN change, 28.3% for AP change, and 65.9% for AK change; Table 1). Vegetation types significantly accounted for 9.3 and 1.0% for soil AN and AP changes, respectively. However, frost status, vegetation index, soil properties, and their interactions weakly contributed to available nutrients changes in topsoils. For example, the interaction of frost status and vegetation types accounted for < 2% for soil available nutrients changes (Table 1). Furthermore, the increasing rates of active layer thickness (ALT) were negatively associated with soil AN change and did not change significantly with AP and AK changes based on the Qinghai-Tibet Highway data (Fig. 5).

The relationships between available nutrients dynamics and environmental factors (Figs. S6–S11), as well as the main factors influencing available nutrients changes, considerably differed under various vegetation types (Table S3). For instance, soil AN changes exhibited no significant correlations with environmental factors in swamp meadow and desert (except for soil pH), while they were slightly related to MAP and N deposition in meadow and steppe (Figs. S6–S7). Similarly, soil AP changes did not correlate with soil properties in swamp meadow and desert, but showed negative relationships with soil properties in meadow and steppe (Fig. S9). Soil AK changes were not associated with soil texture in swamp meadow, whereas they were closely related to soil texture in steppe and desert (Fig. S11). The controlling factors on available nutrients dynamics largely varied among vegetation types, while initial available nutrients (1980s) explained the greatest percentage of total variations in available nutrients changes across the Tibetan grassland (Table S3).

## 4. Discussion

### 4.1. Temporal dynamics of soil nutrient availability

Topsoil AN stock significantly increased by 2.86 $g/m^2$ (24%) across the Tibetan grassland from the 1980s to 2010s (Fig. 2a, d). Soil AN dynamics could be partially attributed to environmental changes in alpine ecosystems. First, changes in vegetation biomass and net primary production (NPP) during the last three decades were hypothesized as responsible for AN variations. Yao et al. (2018) reported that NPP has increased in most area of the Tibetan grassland from 1982 to 2015, with a rate of 0–4 $g\,C\,m^{-2}\,yr^{-1}$. Moreover, NDVI increased significantly in swamp meadow, meadow, and steppe but did not change significantly in desert sites from 1982 to 2010 (Shen et al., 2015). This observation is consistent with the patterns of changes in topsoil AN stock among vegetation types (Fig. 2a, d) in spite of the weak relationship between AN changes and NDVI (Fig. S4). In addition to the enhanced precipitation and temperature reported across the Tibetan Plateau (Yao et al., 2018),

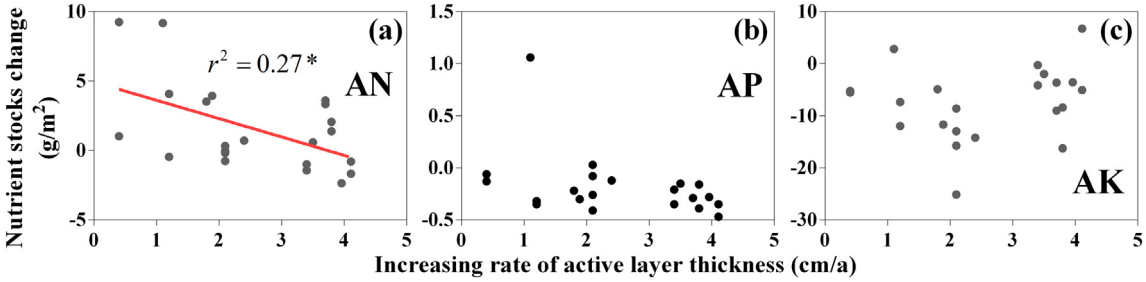


**Fig. 5.** Relationships between available nutrients changes in topsoils (10 cm) and the increasing rates of active layer thickness along the Qinghai-Tibet Highway. AN, available nitrogen; AP, available phosphorus; AK, available potassium; * indicates significant relationship at $P < 0.05$.

the elevated NPP may also be in response to the increased topsoil AN stocks in Tibetan grassland associated with accelerated plant growth and organic matter decomposition rates (Natali et al., 2012). Second, elevated atmospheric N deposition may increase the amount of soil N available for absorption and utilization by alpine plants and soil microbes (Fu and Shen, 2017). A recent synthesis through manipulative experiments suggested that N addition increased soil inorganic nitrogen in alpine soils (Fu and Shen, 2017). However, our results did not confirm these observations, since there are low N deposition rates over the entire Tibetan Plateau (Fig. S4; Liu et al., 2013). The Tibetan Plateau has experienced a significant increase ($P < 0.05$) in wet N deposition during the last thirty years, with an average rate ranging from 5.4 to 6.1 kg N ha$^{-1}$ yr$^{-1}$ (Liu et al., 2015). Conversely, enhanced N deposition may indirectly affect soil N availability through increasing plant N (Liu et al., 2013). Future long-term and ecosystem-scale experiments are necessary to test this hypothesis.

Topsoil AP and AK stocks significantly decreased by 0.02 g/m$^2$ (−3%) and 4.03 g/m$^2$ (−23%) over the Tibetan grassland between the two sampling periods, respectively (Fig. 2). Although AP and AK are directly associated with vegetation productivity and growth, no or weak relationships were observed between changes in these nutrients availability and the NDVI data across alpine grassland (Figs. S4, S6, S8, S10). These results indicate that the occurrence of certain vegetation types may not influence the availability of key nutrients in soils. These findings are in agreement with Tian et al. (2017) who reported an insignificant relation between available nutrients in soils and vegetation types in the eastern Tibetan Plateau. In addition, there were weak correlations between changes in nutrients availability and N deposition (Figs. S4, S6, S8, S10). Fu and Shen (2017) observed that N addition did not affect the AP in alpine soils. Others have also documented that atmospheric P and K deposition rates were much lower in the Tibetan Plateau compared to other regions (Mahowald et al., 2008; Sardans and Peñuelas, 2015) and thus an insignificant contributor to available P and K.

There were large differences in the balance and amount of soil available nutrients among vegetation types between the two sampling periods (Fig. 2). Those differences under various vegetation types indicate that vegetation types can greatly affect the soil nutrients availability dynamics. Our application of general linear models also revealed that vegetation types explained 9.3% for AN dynamics and 1% for AP dynamics, while vegetation types did not account for variations in AK dynamics due to their relatively uniform changes (Table 1; Fig. 2). Soil available nutrients are closely associated with soil moisture content and distribution. In drier regions, lower available water content hinders nutrient utilization and leads to relatively higher AP and AK in soils (Sardans and Peñuelas, 2015). Soil water content and distribution are unique for each vegetation type. In general, increases in soil moisture and plant community productivity are associated with decreases in available soil nutrients (Tian et al., 2017). One example is the observed 3% decrease in available phosphorus stocks among vegetation types provided in Fig. 2, with large variations in changing magnitude among vegetation types. This seems to be ecologically relevant because soil P availability plays a dominate role in altering species diversity and ecosystem production (Fridley, 2002; Hooper et al., 2012). Previous studies have also shown that changes in P availability can modify soil microbial community composition (Liu et al., 2012), affecting the Tibetan ecosystem.

Changes in soil nutrients availability were weakly correlated with soil variables over the Tibetan grassland (Fig. S5). The general linear models demonstrated that soil pH and fine-particles accounted for < 7% of variations in soil available nutrients dynamics among vegetation types (Tables 1, S1). A previous study in the eastern Tibetan Plateau, soil pH and texture had an insignificant impact on soil AP and AK for the topsoil layer (Tian et al., 2017). A moderate relationship between soil texture and water content on migration of available nutrients was established by Whitehead (2000). Coarse texture soils, in general, have higher porosity and associated higher mass flow than finer texture soils. However, finer texture soils typically have slower rates of diffusion, higher available water capacity, and slower movement of available nutrients than coarse texture soils (Whitehead, 2000). Therefore, this could lead to accumulation of available nutrients for topsoils in relatively wetter environments due to plant cycling (e.g. AP: swamp meadow and meadow; Tian et al., 2017) and depletion of available nutrients for the topsoil layer in relatively drier environments due to leaching (i.e. AP: steppe and desert) over time.

### 4.2. *Effects of climate factors on soil nutrient availability dynamics*

Soil nutrients availability changes were also weakly or insignificantly related to MAT and MAP across the Tibetan grassland (Fig. S4). MAT and MAP only explained a small percentage of total variations in soil nutrients availability changes among vegetation types (Tables 1, S1), indicating that climatic variables weakly affect the changes in soil available nutrients. However, increased temperature and precipitation could indirectly influence soil nutrients availability dynamics through altering weathering rates of parent materials and plant growth and productivity. Increasing in temperature and rainfall are thought to enhance rock weathering rates by changing the interaction processes of parent materials with water and other sources (Whitehead, 2000), which releases different amounts of soil nutrients among different climate regimes. By contrast, soil P and K gradually decline in soils through increased leaching as weathering and development of soils continue to occur. Soil N has also been observed to accumulate from enhanced biological N fixation and atmospheric deposition (Camenzind et al., 2018). Our results reflect the magnitude of weathering degree and leaching among vegetation types. Chen et al. (2016) observed accelerated nitrification and denitrification processes associated with increased temperature and precipitation. This relation is likely responsible for the elevated soil AN stock in the swamp meadow, meadow, and steppe vegetation types, and desert type showed an insignificant variation in soil AN owing to its lower MAT and MAP (Wu et al., 2016). The unpredictable pattern of soil AK stocks among vegetation types confirmed that soil K is more easily depleted compared to soil N and P across cold ecosystems (Sardans and Peñuelas, 2015).

Changes in climate conditions could impact plant productivity through altering water availability and its efficiency of use. It has been reported that NPP showed a positively linear relationship with MAT and MAP (Yao et al., 2018), which suggested higher overall productivity of plant growth in warmer and wetter regions (Luyssaert et al., 2007). Based on the above discussions, higher soil nutrient availability is closely associated with higher vegetation production. In addition, water availability plays a crucial role in connecting soil available nutrients and vegetation growth. The roots and soil moisture distribution could affect the vertical distribution of available nutrients in soil profiles, which lead to accumulations of available nutrients for plant growth in topsoils (McCulley et al., 2004; Tian et al., 2017). Therefore, the changing hydrothermal regimes and roots development with climate change, combined with plant cycling that results in different transport of soil nutrients (Tian et al., 2017), resulted in the different patterns of soil available nutrients dynamics across the Tibetan grassland.

### 4.3. Effects of soil variables on soil nutrient availability dynamics

The initial available nutrients measurements proved to be the most valuable environmental observation in terms of explaining soil nutrient dynamics (Fig. 4). This pattern is consistent with several previous studies regarding the relationship between temporal changes of soil organic carbon and original stocks. For example, soil organic carbon (SOC) content tends to decrease over time in regions where SOC content is high. In regions like the southwestern Amazon basin and the northern grasslands of China, where initial levels of SOC are low, SOC levels tend to grow over time (Holmes et al., 2006; Liu et al., 2017). Crowther et al. (2016) found that the warming-induced changes in SOC stocks depended on initial SOC stock, and estimated an overall loss of global soil carbon stocks in upper soil horizons based on this relationship. These results suggest that the magnitude of nutrient dynamics in soils may be largely dominated by the initial levels of nutrient stocks.

Selected environmental factors and their interactions accounted for 32.5% for AN dynamics, 37.9% for AP changes, and 67.5% for AK changes (Table 1). Other environmental factors and measurements, such as microbial activity, changes in plant community structure and productivity, may be responsible for the changes in soil available nutrients, especially for soil AN and AP dynamics due to their close relationships with microbial activity (Richardson et al., 2009). It has been reported that enhanced mineralization of soil organic matter induced by microbial activity could provide significant soil available nutrients for vegetation growth, diminishing the loss of soil nutrients because of leaching or other geochemical reactions and enhancing the possibility of plant uptake (Camenzind et al., 2018). Although some studies addressed the influence of microbial activity on soil nutrients (Richardson et al., 2009; Camenzind et al., 2018), little attention has been paid to the permafrost affected soils under changing environments, and therefore further manipulative experiments are required.

### 4.4. Effects of permafrost degradation on soil nutrient availability dynamics

Permafrost soils hold considerable available nutrients for plant growth (Keuper et al., 2012), which might be released from thawing permafrost (Salmon et al., 2016), thus possibly affecting the plant communities and production (Wang et al., 2017). Our results showed that soil AN stock changes were negatively associated with the increasing rates of active layer thickness (ALT), while soil AP and AK changes were insignificantly related to variations in ALT along the Qinghai-Tibet Highway (Fig. 5). This indicates that topsoil N availability increases higher in regions where permafrost is slightly degraded; in contrast, it increases slightly or decreases in areas where permafrost degradation occurs dramatically. For example, in wet regions, the ALT did not change significantly during the past years due to the insulation effects of organic layers and the protection of dense vegetation (Zhao et al., 2010); however, in dry environments, the ALT increased significantly over the past decades because of either a thin or no organic layers and sparse vegetation (Wu et al., 2015). Moreover, in cold ecosystems, increasing temperature could stimulate microbial decomposition and mineralization in topsoil layers, thus enhancing N availability (Wang et al., 2017).

Deepened ALT may increase the thickness of the root zone, allowing plants to access available nutrients in previously frozen layers and redistributing those nutrients to surface due to plant cycling. This phenomenon has been reported in circumpolar permafrost regions (Wang et al., 2017) but may differ in permafrost soils of Tibetan where the depth of annual thaw is thick. Circumpolar regions have an average ALT of 0.5 m (Mishra and Riley, 2014), while the ALT of permafrost areas of the Tibetan region is larger than 2 m (Pang et al., 2009). In addition, both regions have a similar rooting profile, with approximately 90% of roots concentrating on the topsoil 30 cm soils (Jackson et al., 1996; Yang et al., 2009). Consequently, it is easy for roots to utilize the released nutrients in deep thawing soils that are available for plant growth in circumpolar permafrost regions but difficult in Tibetan grassland. Wu et al. (2016) also argued that the thick active layer might not affect the biogeochemical processes of topsoils in the western Tibetan Plateau. The insignificant correlations of soil AP and AK changes with the variations in ALT may suggest that permafrost degradation does not affect topsoil AP and AK dynamics. The general linear models also showed that frost status did not significantly contributed to topsoil AP and AK dynamics (Table 1). However, these analyses may not ascertain the influence of permafrost degradation on soil available nutrients dynamics, especially on soil AP and AK changes, and thereby in-situ and long-term manipulative experiments are needed to figure out how permafrost changes affect soil nutrients.

## 5. Conclusions

Soil AN significantly increased by 24%, whereas both soil AP and AK significantly decreased by 3% and 23%, respectively, across the Tibetan grassland from the 1980s to 2010s. Topsoil available nutrients dynamics varied considerably among various vegetation types. Initial available nutrients explained 16.4% of soil AN changes, 28.3% of AP changes, and 65.9% of AK changes, and vegetation types accounted for 9.3% of variations in soil AN dynamics, though other variables significantly contributed to soil nutrient availability dynamics. Overall, our findings indicate that vegetation types and initial nutrient contents play key roles in controlling soil nutrient availability dynamics. These results suggest that if climate warming continues to occur, combined with the decoupling of soil carbon and nitrogen from phosphorus and potassium (Tian et al., 2018) and the stoichiometric shift of topsoil C:N:P ratios (Yang et al., 2014) in China's grassland, the nutrient limitation may shift from N-limit to P-limit or K-limit in Tibetan ecosystems, particularly in wet meadow. Overall, our results suggest that permafrost degradation can increase soil N availability, while it does not influence soil P and K availability in Tibetan grassland.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2018.12.009.

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